

## ORIGINAL ARTICLE

# How geographic distance and depth drive ecological variability and isolation of demersal fish communities in an archipelago system (Cape Verde, Eastern Atlantic Ocean)

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Archipelago system; bathymetry; biogeography; ecological variability; fish community structure; geographic distance; isolation factor; multivariate analysis; relative dominance index.

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**Abstract**

Cape Verde is a tropical oceanic ecosystem, highly fragmented and dispersed, with islands physically isolated by distance and depth. To understand how isolation affects the ecological variability in this archipelago, we conducted a research project on the community structure of the 18 commercially most important demersal fishes. An index of ecological distance based on species relative dominance ( $D_i$ ) is developed from Catch Per Unit Effort, derived from an extensive database of artisanal fisheries. Two ecological measures of distance between islands are calculated: at the species level,  $\Delta D_i$ , and at the community level,  $\Delta D$  (sum of  $\Delta D_i$ ). A physical isolation factor ( $I_{db}$ ) combining distance ( $d$ ) and bathymetry ( $b$ ) is proposed. Covariance analysis shows that isolation factor is positively correlated with both  $\Delta D_i$  and  $\Delta D$ , suggesting that  $I_{db}$  can be considered as an ecological isolation factor. The effect of  $I_{db}$  varies with season and species. This effect is stronger in summer (May to November), than in winter (December to April), which appears to be more unstable. Species react differently to  $I_{db}$ , independently of season. A principal component analysis on the monthly ( $\Delta D_i$ ) for the 12 islands and the 18 species, complemented by an agglomerative hierarchical clustering, shows a geographic pattern of island organization, according to  $I_{db}$ . Results indicate that the ecological structure of demersal fish communities of Cape Verde archipelago, both in time and space, can be explained by a geographic isolation factor. The analytical approach used here is promising and could be tested in other archipelago systems.

**Problem**

The concept of geographic structure in marine ecosystems is fundamental for understanding population dynamics, for fisheries management, and for the implementation of conservation measures. The geographic structure of populations generally results from spatial distribution patterns that are related to historic or current barriers between local communities, such as geographic distance, environmental patchiness and environmental gradients that tend to keep populations from mixing freely (Bailey 1997). The geographic structure is often naturally fragmented,

with a large habitat area subdivided into habitat patches. This has a major impact on population dynamics, community structure and ecosystem diversity.

Habitat fragmentation tends to reduce the area of habitat patches and decreases the long-term survival probability of populations and communities. In such habitats, population sizes decrease and have a higher probability of going extinct because of environmental or demographic stochasticity and an increasing vulnerability to external influences (Saunders *et al.* 1991). Several authors refer to empirical knowledge about the evolutionary and adaptive mechanisms underlying the response of populations and

communities to fragmentation (Wiens *et al.* 1993; Diffendorfer *et al.* 1995) and analyse the effects of such phenomena according to spatial scale (Andreassen *et al.* 1998). On one hand, small-scale fragmentation is mainly related to patchy populations characterized by specific life-history and behavioral characteristics like intrinsic growth rate, reproduction, food competition and social organization. On the other hand, large-scale habitat fragmentation affects metapopulation dynamics through processes such as exchange rates between local populations, connectivity, speciation, resource turnover and environmental pressures.

Physical isolation by geographic distance has been proposed to drive genetic isolation and population structure (Wright 1943), not only in marine systems like coral reefs and archipelagos (De Wolf *et al.* 1998, 2000; Planes & Fauvelot 2002; Duda & Rolán 2005), but also in terrestrial ecosystems for birds (Wiggins *et al.* 1998), mammals (Bjørnstad *et al.* 1998), and plants and invertebrates (Zschokke *et al.* 2000). Wright (1943) initially introduced the concept of isolation by distance in an island population structure model where organisms' dispersal ability is constrained by distance and where gene flow is most likely to occur between neighboring populations (Planes & Fauvelot 2002). In parallel, the vertical dimension associated with bathymetry plays a varied and complex role in ecosystem fragmentation through its interaction with hydrodynamic processes such as wind-driven circulation, turbulent mixing processes and buoyancy forces, as described by Werner *et al.* (1997), Jirka (2001) and Johnston & Merrifield (2003). Such mechanisms play major roles in population and community structure of archipelago systems. These systems are usually characterized by a rich endemic marine biodiversity due to their isolation from continents. They often represent unique ecosystems with clearly established spatial limits. Marine species may respond to various aspects of the habitat's fragmentation that influence species richness, abundance, and distribution as well as biomass (Öhman & Rajasuriya 1998). In species with limited dispersal capacity, isolation by distance can occur.

The Cape Verde archipelago is a tropical oceanic ecosystem that is highly fragmented and dispersed, with islands and group of islands physically isolated by depths often >3000 m. Geographic distance and bathymetry, along with other physical factors, likely induce various degrees of isolation between islands. Understanding how isolation in such a naturally fragmented ecosystem affects the overall ecological variability is a key issue for a better understanding of the Cape Verde marine population dynamics, community structure and biodiversity. Such understanding is necessary for planning sustainable marine exploitation. By using an extensive database of artis-

anal fisheries, the present work analyses how geographic distance and depth affect spatial and temporal structure and variability of exploited demersal fish communities of Cape Verde archipelago. It also examines how physical isolation explains the ecological variability among demersal fish communities in an archipelago system that has, until now, received little scientific attention.

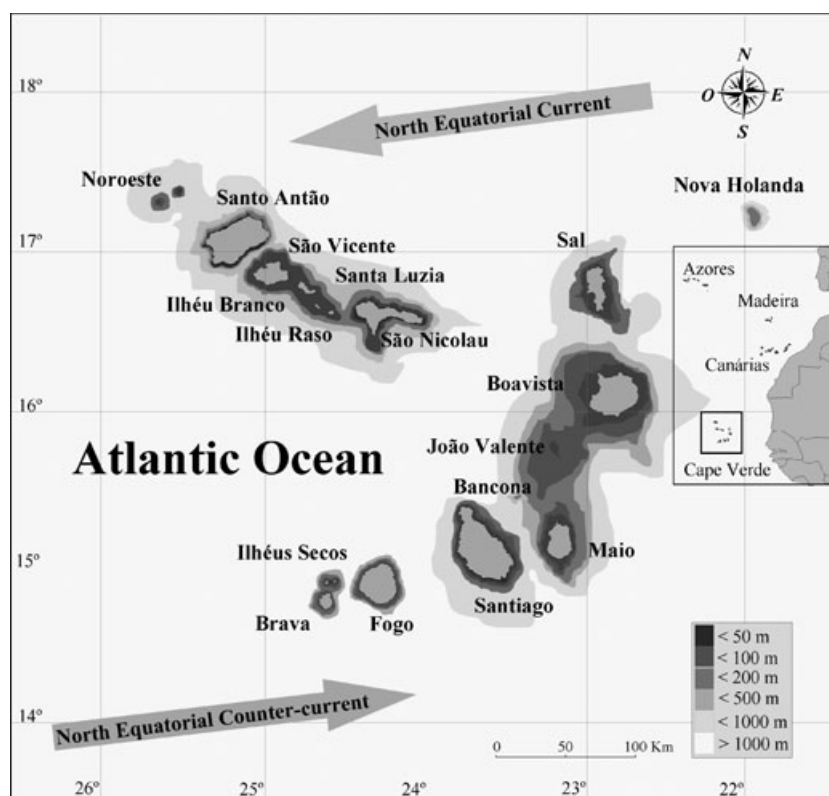
## Material and Methods

### Site description

The Cape Verde archipelago is one of the four oceanic archipelagos belonging to the large biogeographic region of Macaronesia, which also includes Madeira, the Azores and the Canary Islands in the eastern Atlantic Ocean (Fig. 1). With 4033 km<sup>2</sup> of land, 1020 km of coastline and an exclusive economic zone of 734,265 km<sup>2</sup> (Bravo de Laguna 1985), this archipelago is made up of 10 volcanic islands and some islets. Seamounts also come close to the sea surface (Noroeste, Nova Holanda, Bancona and João Valente). The insular shelf slope is steep until 200 m depth and then less pronounced down to 1000 m (Bravo de Laguna 1985). There are a large variety of geographic distances and average depths between islands. The physical environment is largely under the influence of dominant winds. A group of islands, named locally 'Barlavento' [Santo Antão (SA), São Vicente (SV), Santa Luzia (LZ), Ilhéus Raso and Branco (IR), São Nicolau (SN), Sal (SL) and Boavista (BV)], are located windward of the northeasterly trade winds. Another group, named 'Sotavento' [Maio (MO), Santiago (ST), Fogo (FG), Brava (BR), Ilhéus Grande, de Cima and Luis Carneiro (IG); the island abbreviations are used in Fig. 5], are leeward of those winds.

Two main seasons are recognized during the year: a warm one from May to November and a cold one from December to April. The warm season is divided into a dry period between May and July, under the influence of Harmattan wind and dust from the Sahara, and a wet period from August to September, which is influenced by north-easterly Trade Winds from the Azores anti-cyclone and by south-westerly Trade Winds from the Santa Helena anti-cyclone. When rains occur on land, they are torrential, irregular and concentrated in the wet period (90%) according to topography and altitude (De Brum Ferreira 1989). Sea-surface temperature follows the average air temperature, varying from 18 °C to 27 °C during the year.

The islands are also under the strong influence of large-scale oceanic circulation, being on the southern boundary of the North Atlantic's northern anti-cyclonic circulation and on the northern limit of the equatorial counter-current. These two systems of oceanic currents present seasonal variations that affect the circulation of



**Fig. 1.** Location of the Cape Verde archipelago in the biogeographic region of Macaronesia.

the surface layer down to 200 m depth (Stramma & Sie-dler 1988).

#### Data source

The work presented here is based on the artisanal fishery database compiled by the Instituto Nacional de Desenvolvimento das Pescas (National Institute for Fisheries Development from Cape Verde, INDP). That database provides information about fishing boats, fishermen, fishing ground locations, trip date and duration, species identification and catches, from 1996 until the present. The database is supplied by a sampling plan which combines a stratified and a three-stage sampling design for units of unequal sizes as described in Medina (1995).

We used data collected from January 1996 to December 2002. Each landing site was visited six times a month, and all active boats were sampled at each visit providing data on time at sea (in hours), fishing location and catch per fishing trip (in kg) for each species. Knowing the distance between landing ports and fishing sites as well as the average boat speed, time at sea was corrected to provide an estimate of the effective fishing time. Species abundance index was estimated as Catch Per Unit Effort (CPUE). For each island, monthly average CPUE for each species was estimated boat-by-boat as:

$$CPUE = \frac{\sum_{i=1}^n \frac{C_i}{T_i}}{n} \quad (1)$$

where  $C$  and  $f$  are respectively the catch (kg) and the fishing effort (h) of boat  $i$ , and  $n$  is the total number of observations during a month. Artisanal fishing is mainly coastal, practised with hand lines on artisanal wooden and opened boats of standard size between 3 and 6 m, propelled by an outboard engine of 15 HP. Because of technical limitations (storage capacity, communication facilities, *etc.*) fishing units do not have autonomy at sea and thus fishing operations are carried out within a period of 24 h in a limited range area (*c.* 10 km) around islands. In such a tropical ecosystem, demersal fisheries are multi-species; no particular commercial species is targeted and the whole catch is landed at 85 artisanal fishing ports, and sold on local markets. Because of these characteristics of the artisanal fishery, we do not expect variation in fishing power between boats, therefore, no standardization of CPUE was necessary. As original data were expressed in weight, we used biomass of catches rather than number of individuals. These procedure could lead to biases when estimating dominance of larger than average individuals. However, in the structuring of the communities, each individual has an ecological cost

proportional to its biomass (*i.e.* the part of the resources that it takes) as well as an ecological value (*i.e.* its contribution to the stability of the system). Very often, catch samples of demersal fish contain individuals of different lengths and at different stages of maturity and so they represent different ecological cost and value in the structuring of communities. Therefore, the use of biomass units is recommended (Dickman 1968; Wilhm 1968; Lyons 1981; Jin & Tang 1996; Legendre & Legendre 1998).

Winters & Wheeler (1985) present a general criticism in interpreting CPUE data as an abundance index without prior information on population spatial distribution. However, in this research we worked at an island scale. Thus, despite these general criticisms and precaution, we assume that the spatial distribution of CPUE of 1354 standard artisanal boats fishing all year round on the 260 fishing sites dispersed on a cumulative shelf area of 5394 km<sup>2</sup> (Bravo de Laguna 1985) over 7 years, actually reflects the spatial distribution of demersal species and is representative of changes in the area occupied by demersal fish communities. As stated by Greenstreet & Hall (1996), examining fisheries data from a multi-species perspective is important because, for example, exploited species may be replaced by ecologically similar species differing only in their sensitivity to exploitation. So, for the purpose of this work, such a procedure seems quite adequate according to the nature of data available and the peculiarities of the fishery and ecosystem being studied.

### Species selection

For the purpose of this study, the 18 most abundant species were selected (Table 1) from about 40 commercially

important demersal fish. On one hand, such a choice warrants the availability of data for all species under study, and avoids missing values, which enhance the robustness of statistical analyses. On the other hand, dominant species determine the main biological characteristics of demersal communities and the non-target assemblages appear to remain relatively unchanged, despite long-term intensive fishing activity (Colvocoresses & Musick 1984; Greenstreet & Hall 1996; Jin & Tang 1996). Doubtful and false identifications were excluded from the data set, and only data corresponding to the identification level of species were considered.

### Ecological indices

There is much ecological literature that focuses on the concept of species richness, seeking common approaches and frameworks for measuring population, community, and ecosystem variability. All methods aim at reducing the high dimensionality of species abundance data to summarize community structure and each one is sensitive to specific aspects of structural variation. No single measure is therefore adequate to capture all community properties. Thus, according to ecological aspects that one seeks to highlight at a species, community or ecosystem level, it is often of interest to find the approach best adapted to the objectives of the research, able to provide the most robust conclusions. Ecological distance measures allow subsequent ordination methods, statistical approaches widely used in ecology to depict community structure and respective variation in space and time (Legendre & Legendre 1998; McCune & Grace 2002).

For the purposes of the present study, we considered each island as a finite community with several ecological

INDP database code	scientific name	English name	local name
253	<i>Bodianus scrofa</i>	Barred hogfish	Bedja
259	<i>Lethrinus atlanticus</i>	Atlantic emperor	Bica de rocha
260	<i>Epinephelus marginatus</i>	Dusky grouper	Mero
268	<i>Apsilus fuscus</i>	African forktail snapper	Fatcho de fundo
270	<i>Lutjanus agennes</i>	Gorean snapper	Goraz
322	<i>Pseudopenaeus prayensis</i>	West African goatfish	Salmonete
369	<i>Galeoides decadactylus</i>	Lesser African threadfin	Barbo
380	<i>Parapristipoma humile</i>	Guinean grunt	Papagaio
385	<i>Pomadasys incisus</i>	Bastard grunt	Besugo
394	<i>Priacanthus arenatus</i>	Atlantic bigeye	Façola
402	<i>Scarus hoefleri</i>	Guinean parrotfish	Bidião
452	<i>Scorpaena scrofa</i>	Largescaled scorpionfish	Fanhama
457	<i>Cephalopholis taeniops</i>	African hind	Garoupa
465	<i>Mycteroperca rubra</i>	Mottled grouper	Badejo
470	<i>Serranus atricauda</i>	Blacktail Comber	Manelinho
528	<i>Virididentex acromegalus</i>	Bulldog dentex	Bentelha
606	<i>Acanthurus monroviae</i>	Monrovia doctorfish	Barbeiro
699	<i>Seriola dumerili</i>	Greater amberjack	Esmoregal

**Table 1.** List of the main demersal fish species reported in the INDP artisanal fisheries database and selected for the present research.

niches characterized by a particular species richness, equitability and community structure. Therefore, based on the nature of the data available (fishery commercial data), we introduced an ecological index  $D_i$  based on species relative dominance between pairs of islands. Dominance is recognized as an important parameter of community structure that integrates the majority of the mathematical formulations of diversity indices and ecological distance measures (Frontier 1983; Legendre & Legendre 1998; Moullot & Lepretre 2000). To assess the ecological distance between two islands 1 and 2, we defined a relative dominance ( $D_i$ ) of each species ( $i$ ) in each island as the proportion of its biomass  $B_i$  at each island related to the total abundance of all species in the two islands:

$$D_i = \frac{B_i}{B_1 + B_2} \quad (2)$$

where  $B_1$  and  $B_2$  represent the total biomass of all species in each island. As stated by Legendre & Legendre (1998) species are basic units in the theory of the ecological niche, each representing a genetic pool that shares ecosystem suitability and, in doing so, they are structured in communities. We assumed then that the value of  $D_i$  over space and time might be an indicator of variation in ecosystem suitability as perceived by a particular species and is an imprint of the community structure. The contribution of each species to the ecological distance between communities from two islands is the absolute value  $\Delta D_i$ :

$$\Delta D_i = \frac{|B_{i,1} - B_{i,2}|}{B_1 + B_2} = |D_{i,1} - D_{i,2}| \quad (3)$$

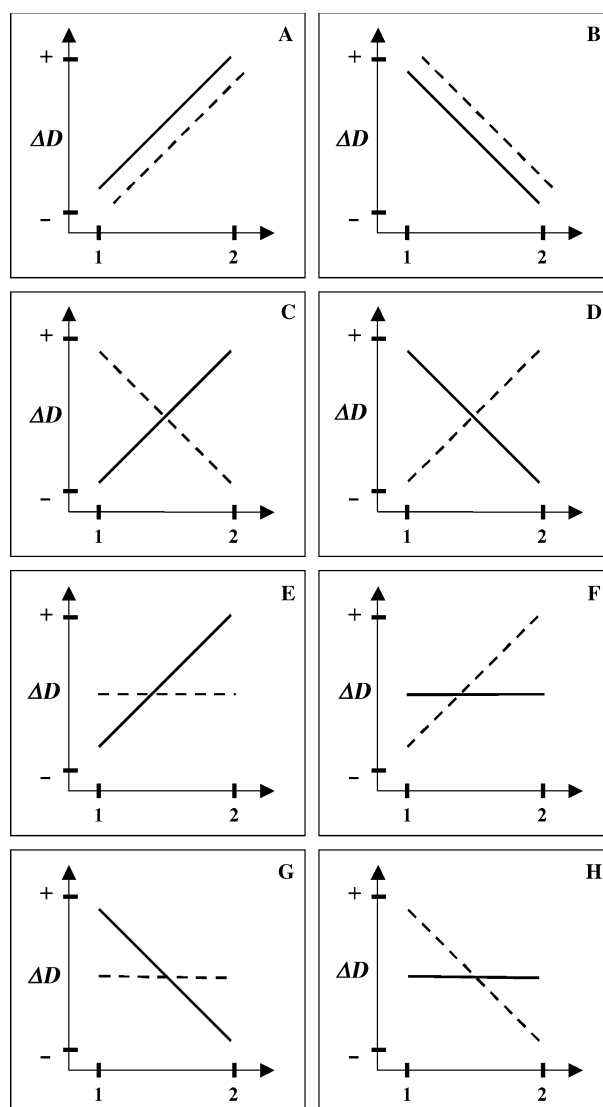
Then we define an index of ecological distance between two islands,  $\Delta D$  as the sum of  $\Delta D_i$  for the  $n$  species recorded on the two islands:

$$\Delta D = \sum_{i=1}^n \Delta D_i \quad (4)$$

$\Delta D$  became a particular expression of Steinhaus's coefficient (Legendre & Legendre 1998). It varies between zero and unity respectively from identical to completely different community structure.

#### Effect of distance and bathymetry

In order to better understand how geographic distance and bathymetry can be integrated to explain ecological variability among islands, we propose a conceptual covariation model for the most probable scenarios (Fig. 2). In some cases, geographic distance may strengthen the bathymetric effect (positive covariance) by inflating isolation and variability between ecosystems (Fig. 2A and B).



**Fig. 2.** Conceptual model to explain the effect of geographic distance (---) and bathymetry (—) on species relative dominance ( $D_i$ ) and community structure variation among islands in an archipelago system. For a potentially dominant species,  $D_i$  between islands 1 and 2 may be affected by positive covariance (A and B), negative covariance (C and D), partial positive correlation (E and F) or partial negative correlation (G and H).

In other cases, geographic distance may counteract the bathymetric effect (negative covariance) either by reducing isolation and ecological variability between ecosystems (Fig. 2C) or by increasing isolation (Fig. 2D). Furthermore, particular situations exist where one of those variables masks the positive or negative effect of the other. This is the typical situation of suppressor variables, first introduced by Horst (1941) and widely reported in the scientific literature (Lancaster 1999; Mackinnon *et al.* 2000; Lynn 2003). Despite considerations about the

deleterious effect of colinearity between independent variables and the recommended statistical procedures to exclude one of them from computations (Zar 1984), the computation of a first-order partial correlation has been recommended (Jolicoeur 1997; Legendre & Legendre 1998) in order to better describe the relationships between variables. It is then possible to distinguish between a positive (Fig. 2E and F) or negative (Fig. 2G and H) effect.

In the present work, the shortest geographic distances between pairs of islands ( $d$ ), expressed in kilometers (km), were obtained by direct measurement on the Cape Verde archipelago map published by the United Kingdom Hydrographic Office (1989). Distances ( $d$ ) varied from 6 km, between Brava island and Secos islets, to 270 km, between Santo Antão and Maio islands. Average isobaths, expressed in meters (m), were obtained from Bravo de Laguna (1985) and data issued by IOC, IHO & BODC (2003). The mean depth between pairs of islands ( $b$ ) was then calculated and it varies from 55 m between Brava island and Secos islets to 3990 m between São Vicente and Fogo islands.

We investigated the relationship between species relative dominance ( $D_i$ ), the geographic distance ( $d$ ) and the average bathymetry ( $b$ ). Islands were first compared two by two. A time series of  $D_i$  was calculated for each island, over the entire period and for all species. The two series of  $D_i$  were compared by a Pearson correlation analysis. A pair of islands was then characterized by (i) the correlation coefficient between  $D_i$ , (ii) the geographic distance ( $d$ ), and (iii) the average bathymetry ( $b$ ) between those islands. For the entire system, those parameters are represented in three square matrices that were compared by a series of Mantel tests (Dietz 1983; Smouse *et al.* 1986; Oden & Sokal 1992), which provided total and partial correlations between those three matrices. In order to meet conditions of normality,  $D_i$  values were  $\log_2$  transformed. Missing values and double zeros were excluded from computations.

Finally, to integrate mutual influence of distance and depth, we computed a physical isolation factor ( $I_{db}$ ) as:

$$I_{db} = d \times b \quad (5)$$

Computed values of  $I_{db}$  varied from 0.33 km<sup>2</sup> between Brava island and Secos islets to 846 km<sup>2</sup> between Sal and Brava islands. In order to prevent scale measures effects, for statistical analysis  $I_{db}$  data were normalized.

#### Spatial and temporal variability

First, we tested main effects on  $\Delta D_i$  of year (Y, seven levels), month (M, 12 levels) and species (S, 18 levels) with a three fixed-factor ANOVA without replication.

Secondly, we investigated ecological variability between islands at two levels of organization (species and communities) with a series of analyses of covariance (ANCOVA). In a preliminary step, we carried out an ANCOVA between  $\Delta D_i$  as the dependent variable and  $I_{db}$  as covariates for two factors (18 species levels – S, and 12 months levels – M) as independent qualitative variables. That analysis allowed us to define species groups and seasons. Next, we computed an ANCOVA between  $\Delta D$  and  $I_{db}$  for those species groups (C: two levels) and for seasons (P: two levels).

Multivariate analyses were used to illustrate the spatial organization of the demersal fish community in the archipelago. The matrix of monthly average  $\Delta D_i$ , with the 12 islands as observations and the 18 species as descriptors, was analysed with a principal component analysis (PCA) based on the Pearson correlation coefficient. To complement this analysis, we performed an agglomerative hierarchical clustering (AHC) for the same data matrix. Although single linkage is widely used as an agglomerative method to complement PCA (Legendre & Legendre 1998), we used a complete linkage method because we were mainly interested in a better contrast between islands or island groups. Finally, a complementary analysis of islands and species in the space of the first two PCA axes enabled us to study the variability between islands and the correlations between species in addition to the relationships between islands and species. For all statistical tests the null hypothesis was analysed for an  $\alpha$  error of 0.05. All statistical calculations were made with the XLSTAT-Pro v.7.5.3 software.

## Results

#### Relationships between $D_i$ , $d$ and $b$

Linear correlations were not significant between  $D_i$  and  $d$  and between  $D_i$  and  $b$  but, highly significant between  $d$  and  $b$  (Mantel tests, Table 2). Partial correlation was highly significant as well between  $D_i$  and  $d$  as between  $D_i$  and  $b$ . It suggests that  $d$  and  $b$  interact as suppressor

**Table 2.** Linear and first-order partial correlations (in bold) from a Mantel test computed between three symmetrical matrices ( $r$  correlation between  $\log_2 D_i$ ), (geographic distance  $d$ ) and (average depth  $b$ ). Tests were performed for an exhaustive number of permutations.

matrix	linear correlation	partial correlation	P
$\log_2 D_i \times b$	0.156	–	0.11
$\log_2 D_i \times d$	0.077	–	0.441
$b \times d$	0.945	–	<0.0001
<b><math>\log_2 D_i \times d   b</math></b>	–	<b>0.779</b>	<b>&lt;0.0001</b>
<b><math>\log_2 D_i \times b   d</math></b>	–	<b>–0.698</b>	<b>&lt;0.0001</b>

variables, masking a larger and significant correlation between each one of them and  $D_i$ .

Positive partial correlation between  $D_i$  and  $d$ , on one hand, and negative partial correlation between  $D_i$  and  $b$ , on the other hand, show that, for potentially dominant species, distance and depth do not affect community structure in the same way (Table 2). Increasing the geographic distance while average depth remains constant will increase  $D_i$  (positive partial correlation); reciprocally, increasing the average depth while geographic distance remains constant will decrease  $D_i$  (negative partial correlation).

#### Relation between $\Delta D_i$ , $\Delta D$ and $I_{db}$

Results indicate that  $\Delta D_i$  is highly related to species, year and month (ANOVA, S:  $F_{17,7845} = 473.23$ ,  $P < 0.001$ ; Y:  $F_{7,7845} = 37.181$ ,  $P < 0.001$ ; M:  $F_{11,7845} = 233.626$ ;  $P < 0.001$ ). Monthly patterns are consistent between years (interactions between Y and M:  $F_{66,7845} = 0.917$ ,  $P = 0.484$  n.s.). Despite a year effect, no particular trend was observed in the time series. However, S and Y show significant interaction ( $F_{187,7845} = 7.295$ ,  $P = 0.000$ ) illustrating the existence of a strong monthly pattern in  $\Delta D_i$ , common to all species.

Following these results, to assess relationships between  $\Delta D_i$  and  $I_{db}$ , further analyses were carried out on an 'average year', calculated from monthly averaged  $\Delta D_i$ . We observe a significant effect of month and species on the covariance between  $\Delta D_i$  and  $I_{db}$  (Table 3, upper panel). By evaluating the significant amount of information brought by each variable and parameter to the model, we distinguish two seasons ( $P_1$ : January, February, March, April, and December;  $P_2$ : May, June, July, August, September, October, and November) and two discrete species

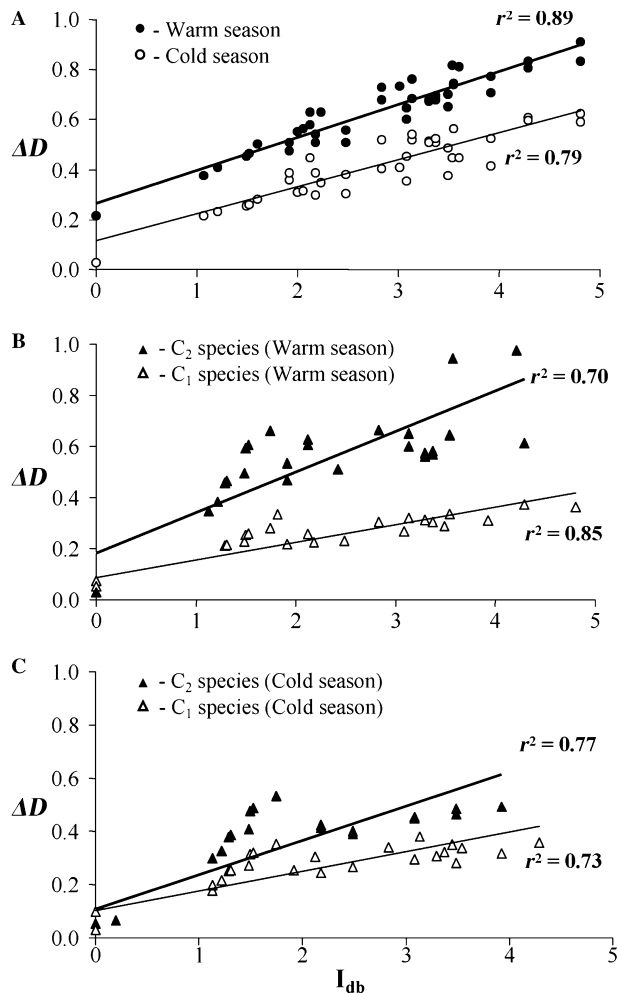
groups ( $C_1$ : 253, 259, 270, 322, 369, 402, 606;  $C_2$ : 260, 268, 380, 385, 394, 452, 457, 465, 470, 528, 699; see species' identifications in Table 1).

Then,  $\Delta D$  was computed between islands for the two defined seasons (two levels –  $P_1$  and  $P_2$ ) and species groups (two levels –  $C_1$  and  $C_2$ ), and its spatial and temporal variability was studied by further ANCOVA (Table 3, lower panel). Results indicate a significant covariance between  $\Delta D$  and  $I_{db}$ , which is different between seasons and between species groups. It is particularly interesting to note that using seasons (P) and species groups (C) instead of month (M) and species (S) does not cause any significant deviation from the general covariance model, which shows the robustness of our approach. On one hand, a main seasonal effect and the absence of interaction between P and  $I_{db}$  reveal an important influence of  $I_{db}$  on the ecological distance  $\Delta D$  between islands, not varying from one season to another. On the other hand, a significant interaction between species groups and  $I_{db}$  suggests that those groups do not follow the same pattern. Species seem to behave differently in the same season.

The whole statistical analysis led us to a general covariance model illustrating the influence of  $I_{db}$  on  $\Delta D$  between islands. The ecological distance between islands varies between two seasons, being higher during the warm than the cold season (Fig. 3A, Table 4). Within each season one group of species ( $C_1$ ) was less sensitive to the isolation factor ( $I_{db}$ ) than the other one ( $C_2$ ) (Fig. 3B and C, and Table 4). The seasonal pattern is illustrated by the variation of the ecological distance index  $\Delta D$  averaged by month from January to December (Fig. 4); the index is lower during the cold season. According to the standard deviation,  $\Delta D$  seems to be more stable during the warm season.

**Table 3.** Results from the ANCOVA between  $\Delta D_i$  (species level) and  $\Delta D$  (community level) as dependent variables and  $I_{db}$  as covariates. The upper panel of the table shows months (M) and species (S) effects. The lower panel shows season (P) and species group (C) effects.

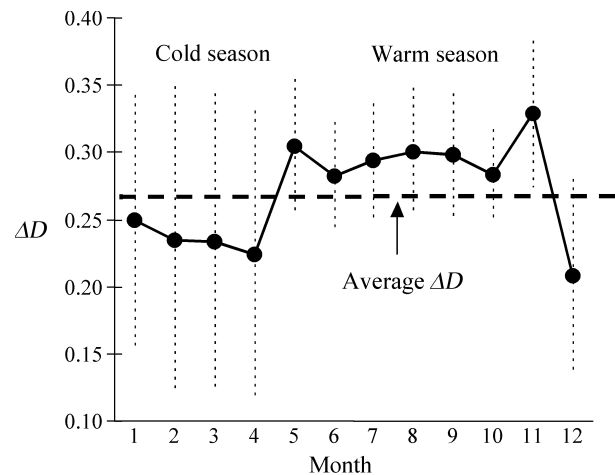
dependent variable	source	df	sum of squares	mean square	Fisher's F	P
$\Delta D_i$ ( $r^2 = 0.619$ )	$I_{db}$	1	163.988	166.351	5626.995	<0.0001
	M	11	43.046	3.272	134.279	<0.0001
	S	17	34.009	2.282	68.644	<0.0001
	$M \times S$	187	3.737	0.019	0.686	0.999
	$M \times I_{db}$	11	0.409	0.040	1.276	0.231
	$S \times I_{db}$	17	0.331	0.019	0.668	0.837
	Error	4742	138.196	0.029		
$\Delta D$ ( $r^2 = 0.806$ )	$I_{db}$	1	2.224	2.224	265.634	<0.0001
	P	1	1.711	1.711	204.324	<0.0001
	C	1	0.530	0.530	63.356	<0.0001
	$P \times C$	1	0.019	0.019	2.267	0.135
	$P \times I_{db}$	1	0.007	0.007	0.795	0.374
	$C \times I_{db}$	1	0.033	0.033	3.962	0.049
	Error	122	1.022	0.008		



**Fig. 3.** Covariance models between community structure variation ( $\Delta D$ ) and physical isolation  $I_{db}$  among Cape Verde islands according to temporal patterns with two different seasons: cold from December to April and warm May to November (A) and species groups showing two levels of sensitivity (B and C).

### Island and community structure

Results of the PCA and of the AHC, illustrated by a Wrocław diagram, show a clear geographic pattern of monthly average species'  $\Delta D_i$ . Islands are grouped accord-



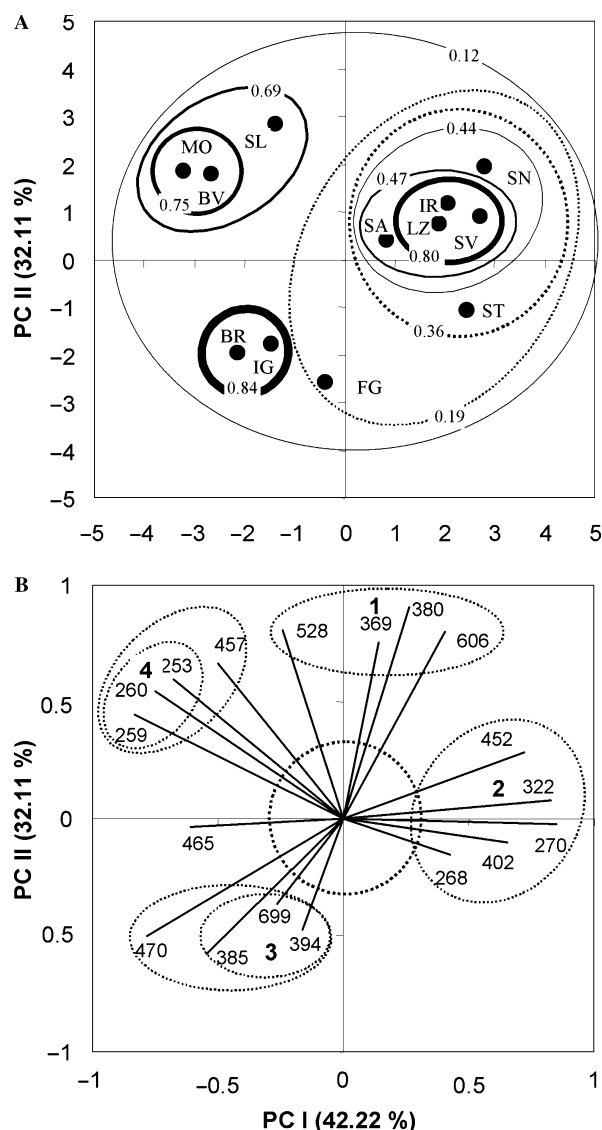
**Fig. 4.** Monthly variation of ecological distance ( $\Delta D$ ). Two main seasons are illustrated: cold, from December to April, more variable, with lower level of  $\Delta D$  and a negative trend; warm, from May to November, with a higher level of  $\Delta D$  and apparently more stable.

ing to degree of physical isolation and ecological similarities (Fig. 5) and species are assembled according to their contribution to the ecological distance between islands. Moreover, a superposition of the two factorial spaces (islands and species) in the PCA led us to recognize a significant association between islands and species (Fig. 6). At a high similarity level ( $\geq 0.80$ ), a group is formed by Brava and the Secos islets, in the southern part of the archipelago, and another one by São Vicente, Santa Luzia and Raso islet in the northern part. Those two island groups are well correlated but, in an opposite way, explaining 42.2% of the total variance. Such a correlation seems to be related to two different species assemblages. While the northern group appears to be more associated with *Apsilus fuscus* – 268, *Lutjanus agennes* – 270, *Pseudupeneus payensis* – 322, *Scarus hoefleri* – 402 and *Scorpaena scrofa* – 452 (assemblage 1), the southern group is better characterized by *Serranus atricauda* – 470, *Pomadourus incisus* – 385, *Priacanthus arenatus* – 394 and *Seriola dumerili* – 699 (assemblage 3). In the east, Sal, Boavista and Maio form another group at 0.69 similarity, but Maio and Boavista are more strongly linked, with a

**Table 4.** Covariance model parameters and adjusted  $r^2$  for different levels of variability between seasons and species' sensitivity to ecological isolation.

parameters	general model		more sensitive species ( $C_2$ )		less sensitive species ( $C_1$ )	
	cold season ( $P_1$ )	warm season ( $P_2$ )	cold season ( $P_1$ )	warm season ( $P_2$ )	cold season ( $P_1$ )	warm season ( $P_2$ )
elevation	0.114	0.265	0.110	0.184	0.101	0.088
slope	0.326	0.395	0.386	0.476	0.205	0.222
adjusted $r^2$	0.794	0.891	0.771	0.703	0.731	0.849





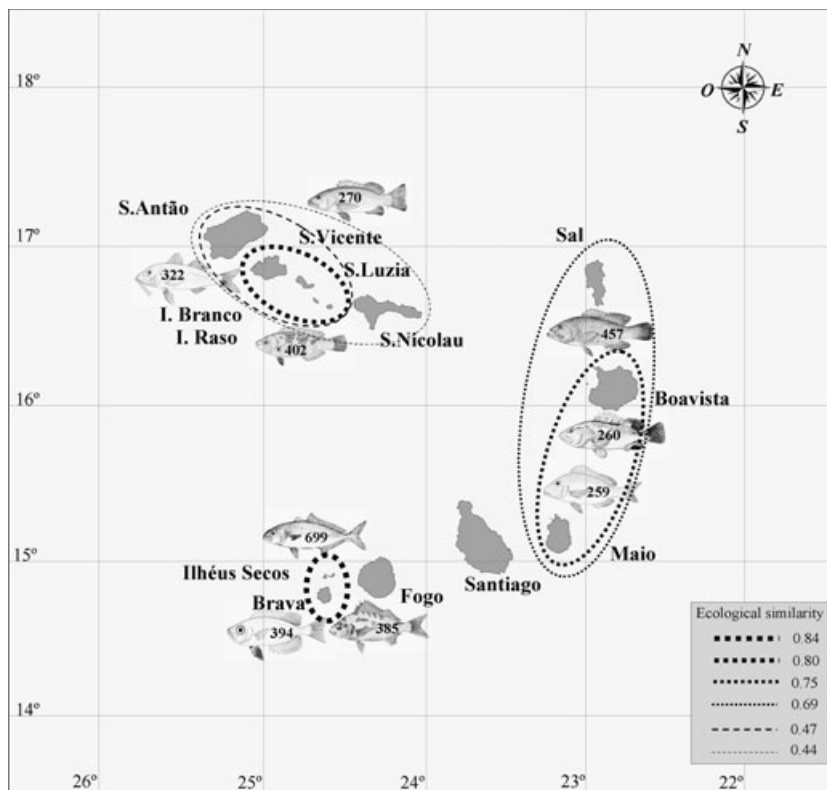
**Fig. 5.** Spatial patterns among Cape Verde islands as determined from a PCA and HAC computed with a Pearson correlation matrix based on the  $\Delta D_i$  from 18 demersal fish species. A: Island structure according to the first two axes, explaining 74.3% of total variance, and a Wroclaw diagram drawn for different levels of similarity (see text for island identifications). B: Species correlation according to the two first axes. The circle (radius  $= \frac{\sqrt{2}}{d}$ ;  $d$  = species number) represents the balanced contribution of species to the two axes (thick dashed line). Numbers in bold represent fish assemblages, other numbers represent species codes (see Table 1).

higher similarity (0.75). This group appears to be associated with *Bodianus scrofa* – 253, *Lethrinus atlanticus* – 259 and *Epinephelus marginatus* – 260 (assemblage 4). *Cephalopholis taeniops* – 457 is weakly linked to this assemblage and seems well correlated with Sal island. This latter island species association explains 32.1% of the total

variance. In almost complete contrast to assemblage 3, species from assemblage 1 (*Parapristipoma humile* – 380, *Galeoides decadactylus* – 369, *Virididentex acromegalus* – 528 and *Acanthurus monroviae* – 606) can be considered intermediate between assemblage 2 and 4 in structuring the northern and eastern island groups. At lower similarities, Santo Antão and São Nicolau tend to be linked with the northern group, while Santiago and Fogo islands, remain isolated. The species *Mycteroperca rubra* (465) is strongly and negatively correlated with assemblage 2, but does not belong to any assemblage.

## Discussion

A large variety of ecological indices are used to assess ecological variability and community structures. In the present research, we used an ecological index based on species relative dominance that also measures species contribution to community structure variation between two islands. Such contribution is measured by the relative dominance of each species on the total species biomass of the two communities. This approach was the most appropriate given the nature of the available data. Interpreting community structure based on commercial fisheries data can be distorted because these data are neither random nor exhaustive and fished communities cannot be assumed to function naturally. In fact, commercial fisheries result from a complex interaction among several factors related to fishers' strategy (Saltaug & Godø 2001). Even in the situation of a mixed fishery (Ketchen 1964; Chadwick & O'Boyle 1990), the data do not represent all species from exploited communities. However, in the system under study, artisanal fishermen sample the fish density around islands in a time invariant process without definite fleet tactics. In such a case where fishing process does not change, CPUE data can be used to construct a time series of comparable abundance indices (Petitgas 1998). The monthly and annual variation patterns of these indices on the main fishing grounds can be indicative of a population's complexity and allow the assessment of spatial and temporal variations in abundance (Begg & Waldman 1999). Thus the use of classical approaches, either synthetic measurements like the Shannon–Weaver, Simpson, Hill and McIntosh indices (Frontier 1983; Legendre & Legendre 1998) or analytical procedures like rank-frequency diagrams (Frontier 1983; Mouillot & Lepretre 2000), are not very useful in such a situation because of their sensitivity to species richness. The approach we propose in the present study to assess community structure variation has the advantage of being mainly sensitive to species abundance distribution rather than to species richness and so is useful in a context where only fisheries data are available.



**Fig. 6.** Map of ecological similarity derived from PCA analysis among demersal fish populations from Cape Verde Islands showing pattern of ecological variability, driven by a physical isolation factor (geographic distance and average depth). For illustration purpose, only the most discriminating species are represented (see Fig. 5 and Table 1).

The relationship among species relative dominance, geographic distance and average depth allow us to highlight an important ecological feature of the species–habitat dynamics in the Cape Verde archipelago that may be applicable to similar systems. Depth and distance are partially correlated with species relative dominance but in opposite ways, which led us to propose a niche effect associated with variation in shelf area and thus, in space availability. On one hand, increasing geographic distance with a constant average depth means more space available and thus improves general suitability of the habitat for potentially dominant species in a particular area. Consequently  $D_i$  will increase. On the other hand, an increase in the average depth for the same geographic distance would decrease the space available and reduce general habitat suitability. As a result,  $D_i$  will decrease because a species has less space available to express its dominance. From the ecological point of view, since space availability is the physical support of biotic and abiotic conditions within which the species can exist, such aspects seem to be important for the dynamics of species' use of space and are related to ecosystem resource partitioning. Hence, it seems to be an important factor structuring demersal fish assemblages. This rationale corresponds to the MacArthur (1957) hypothesis about environment structure and relative abundance of birds in an equilibrium or

near-equilibrium population. However the present study considers two spatial scales: (i) at a island scale, niches seem to be continuous and non-overlapping and (ii) at a archipelago scale, niches are obviously discrete.

The rate of expansion and contraction of a population within a distribution area is unlikely to be uniform as habitat conditions will be less favorable at the extremes than at the centre (Winters & Wheeler 1985). In terms of the amount and arrangement of favorable habitats, the spatial correlation between geographic distance and depth is particularly important in determining the overall suitability of the environment (Hiebler 2000). In a heterogeneous and naturally fragmented landscape like the Cape Verde archipelago, this is particularly important for theoretical studies on the dynamics of population abundance and density (MacCall 1990; Petitgas 1998; Hiebler 2000).

The computation of a physical isolation factor based on geographic distance and average depth between islands allows the integration of their effects and mutual interactions into a single variable whose covariance was tested against community structure variation indices. The rejection of the null hypothesis with such an approach has suggested that, for the Cape Verde archipelago, physical isolation is an important factor that drives ecological isolation among islands. Such ecological isolation varies through the year according to two distinct seasons that

are separated by different wind and temperature regimes. The shorter cold season from December to April seems to be more unstable and shows lower ecological variability than the warmer one, from May to November, which appears to be more stable. This observation leads us to formulate the hypothesis that, in the Cape Verde archipelago, ecological isolation between islands is affected by different hydrodynamic regimes between cold and warm seasons. This dynamic process would be regulated, *inter alia*, by the correlation between the average depth and the distance between islands. Although this assumption will have to be validated by knowledge of oceanic circulation around Cape Verde islands, such information does not yet exist. However, it is well known that wind and temperature variations favor turbulent mixing processes in the water column as well as near the bottom (Spall 2000; Jirka 2001; Johnston & Merrifield 2003) and in archipelago systems, these processes are frequently related to jet current flows between islands (Xie *et al.* 2001).

For the species considered, physical isolation does not affect their relative dominance with the same intensity during the same season. We could distinguish between more sensitive species, dominated by Serranidae (*C. taeniops*, *S. atricauda*, *M. rubra* and *E. marginatus*) and Haemulidae (*P. humile* and *P. incisus*), followed by six other families, each one represented by a single species, and less sensitive species, represented by seven families with one species each. These differences in behavior can be related to interactions between spatial and temporal features affecting their distribution. Species with coastal and shallow distributions throughout the year are expected to be less sensitive than those with a broader and deeper distribution. However, these demersal fishes are mostly sedentary and reef-associated, colonizing rocky or sandy bottoms on the coastal zones around islands. Thus, at least at the juvenile stage, such different behaviors with respect to ecological isolation would be complex to understand. However, species dispersal capability can vary with development stage. Thus, we hypothesize that the main significant interactions between physical and hydrodynamic features that affect species dispersal and distribution probably occur during spawning or early life stages. For the Cape Verde archipelago, no information exists about flows of energy, materials, or organisms across island boundaries. This is a major aspect of the theory of island biogeography (MacArthur & Wilson 1967), and its generalization in neutral theory (Hubbell 1997, 2001). Aside from the recent debate on these theories, both supportive (Volkov *et al.* 2003; Hubbell 2006) and critical (McGill 2003; Wootton 2005), the main assumption of ecological equivalence in communities constrained by dispersal and recruitment seems to limit the applicability of such theories in very heterogeneous

and dynamic systems like coral reefs (Dornelas *et al.* 2006) or archipelagos such as Cape Verde. However, future research on this matter can contribute understanding of ecological variability in the context of functional ecology and the design of appropriate conservation and management strategies.

Community structure shows a geographic pattern according to the physical isolation factor, which suggests that demersal communities are affected by geographic distance and depth. Similar results have been found recently for the genetic structure of gastropod populations (*Conus* sp.) in the eastern Cape Verde islands (Duda & Rolán 2005). These authors found that species from Boavista and Maio islands are genetically more similar to each other than they are to species from Sal islands. In fact, the migration of species between Boavista and Maio has apparently been more common than between Sal and Boavista. This phenomenon seems to be facilitated by stronger ecological isolation ( $I_{db}$ ) between the two latter islands. Despite the importance of oceanographic influences on larval dispersal and their consequences for population connectivity (Werner *et al.* 1997; Cowen 2002), we believe that the long-term persistence of such physical isolation between islands might be at the origin of important speciation processes, resulting in high marine biodiversity at the genetic, specific, taxonomic, ecological and functional levels.

Because there has been no other scientific research on the population structure among the Cape Verde islands related to how fishing affects genetic resources and biodiversity, we suggest that, for conservation and management purposes, populations from spatially distinct islands or islands groups, as identified in the present study, should be considered as discrete management units. As stated by Stephenson (1999), aside from the debate on the basic premise behind the modern concept of a stock (Booke 1999; Swain & Foote 1999), this is particularly important as part of a precautionary approach to fisheries management (FAO 1995) and to topical discussions of the potential value of Marine Protected Areas.

Several physical and geographic features are common among archipelagos from the large biogeographic region of Macaronesia (Cape Verde, Madeira, Azores and the Canary Islands). It would be interesting to test the approach we propose here in a broader context in order to study ecological variability and demersal population structure in the context of archipelago systems. However, the spatial and temporal patterns of the hydrodynamic features that are expected to influence ecological isolation must be included in such a research program.

Among significant scientific questions to be addressed related to geographic distance, depth and ecological isolation in the study area, it will be of great interest to

investigate the population spatial dynamics of the main demersal species on the insular shelf and how they can be related to seasonal and annual variations in population abundance. In order to prevent and control the unknown effect of fishing, it would be desirable to combine commercial fisheries and survey data (Fox & Starr 1996; Petitgas *et al.* 2003; Verdoit *et al.* 2003). Furthermore, to address how such ecological isolation affects population genetic structure and dynamics, more data are needed on the population genetics of marine species in the archipelago. Although recent research has begun to address this issue (De Wolf *et al.* 1998, 2000; Duda & Rolán 2005), these studies were mainly concerned with molluscs. Because of the ecological complexity of such tropical oceanic systems, it will be advantageous to direct research efforts toward a greater diversity of taxa.

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